Wilson Bull., 114(1), 2002, pp. 20–37

SPECIES LIMITS IN OLIVE-BACKED FOLIAGE-GLEANERS (*AUTOMOLUS*: FURNARIIDAE)

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ABSTRACT.—New information on the vocalizations and behavior of populations of the Olive-backed Foliage-gleaner (*Automolus infuscatus*), along with analysis of biometric and plumage characters, reveal that it actually consists of at least two biological species: a form that is restricted to southeastern Amazonia, south of the Amazon and east of the Rio Madeira; and a group that occupies much of the remainder of humid lowland forest in Amazonia and the Guianan region. The southeastern form, although cryptically similar morphologically to other southern Amazonian subspecies of *Automolus infuscatus*, is highly differentiated in all vocal characters. Its distribution overlaps the Rondônia, Pará, and Belém centers of endemism. The remainder of the populations currently considered part of the *infuscatus* group are further differentiated into two subgroups: a northern Guianan group and a southern-western group, the member taxa of which are weakly differentiated from one another, but which differ from members of the other group in plumage, biometric, and vocal characters. The significance of these differences with respect to species limits may depend on the species concept used. Current evidence would support recognition of the two groups as separate phylogenetic species in addition to the southeastern species, but is considered insufficient to support recognition of more than two species under a biological species concept.

Received 10 January 2001, accepted 25 May 2002.

The genus *Automolus* is a group of fairly large, mostly drab plumaged foliage-gleaners (subfamily Philydorinae), which comprises 6–11 species. Vaurie (1980) included the species *rectrirostris* and *erythrocephalus* in his expanded view of the genus, but most recent authors (Peters 1951; Meyer de Schauensee 1966, 1970; Ridgely and Tudor 1994) have recognized those two species in the separate genus *Hylocryptus*. Kratter and Parker (1997) convincingly demonstrated that *dorsalis* belongs with *Anabazenops* rather than *Automolus*, and strong arguments have been made for the transfer of *ruficollis* from *Automolus* to *Syndactyla* (Parker et al. 1985, 1995; Fjeldså and Krabbe 1990; Ridgely and Tudor 1994). More work also is needed to clarify the relationships of *Automolus roraimae*, whose inclusion in the genus has been questioned (Ridgely and Tudor 1994, Kratter and Parker 1997). This leaves a core of six currently recognized species (*leucophthalamus*, *infuscatus*, *rubiginosus*, *ochrolaemus*, *rufipileatus*, and *melanopezus*) comprising the genus *Automolus*.

One of the most widespread members of the genus is the Olive-backed Foliage-gleaner (*A. infuscatus*), which inhabits lowland humid forest throughout much of Amazonia and the Guianan region. Although there are five named subspecies of *A. infuscatus* (Peters 1951), geographic variation within the species has been categorized as "slight" and "not significant" (Vaurie 1980), and no recent authors of either technical works or popular field guides have commented on it.

In August 1991, while conducting field work in the Alta Floresta region of Mato Grosso, Brazil, I noticed the local population of Olive-backed Foliage-gleaners (*A. i. paraensis*) varied dramatically in songs and calls from populations with which I was familiar in Venezuela. Subsequent communication with colleagues revealed that in 1986, T. S. Schulenberg and D. F. Stotz had tape recorded unfamiliar voices of Olive-backed Foliage-gleaners from the middle Rio Jiparaná in eastern Rondônia, Brazil, that matched those I had recorded at Alta Floresta. T. A. Parker also had independently noted the vocal distinctiveness of the Alta Floresta birds on his first trip to the region in 1989 (T. A. Parker pers. comm.). Intrigued by the vocal distinctiveness of birds that appeared, under field conditions, to be "typical" Olive-backed Foliage-gleaners in plumage characters, I began investigating vocal and morphological variation among all of the recognized subspecies in the complex.

In this paper I present new evidence of vocal differences among populations of Olive-

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backed Foliage-gleaners, and re-evaluate geographic variation in plumage and biometric characters within the species. I demonstrate that the subspecies *A. i. paraensis* is sufficiently differentiated to be considered a biological species distinct from other members of the group.

METHODS

I observed and tape recorded "Olive-backed" Foliage-gleaners near Alta Floresta, Mato Grosso, Brazil (yearly visits in August, September, or October, 1991–1999); at Caxiuanã Forest Reserve, Pará, Brazil (August 1999); at São Gabriel da Cachoeira, Amazonas, Brazil (January 1995 and August 1999); Tiputini Biodiversity Station, Napo Province, Ecuador (August 1996); Tambopata Research Center, Madre de Dios, Peru (August 1994); and at multiple sites in Amazonas, Brazil (1991–2000) and edo. Amazonas and edo. Bolívar, Venezuela (1991–1998). All measurements used in behavioral data (distances, heights, etc.) are estimates. Mapped distributions in this paper are based on label data from specimens that I examined, and by more recent records documented with tape recordings. These localities, along with the type localities for each taxon, were entered into a geographic information system (Isler 1997) and mapped by M. L. Isler.

I assume that vocalizations of foliage-gleaners, like those of other suboscines, are mostly or entirely inherited (Kroodsma 1984, 1989; Kroodsma and Konishi 1991), and consequently provide potentially important characters for systematic study (Lanyon 1978, Isler et al. 1997, Krabbe and Schulenberg 1997, Zimmer 1997). To analyze vocalizations, I assembled recordings of *Automolus infuscatus* from across its geographic range, made auditory comparisons, and visually compared spectrograms of all individuals recorded. Songs selected for illustration as spectrograms in this paper were deemed representative based on visual comparison of spectrograms of the large sample. I also examined my own collection of recordings of songs and calls of *A. leucophthalamus*, *A. rubiginosus*, *A. ochrolaemus*, *A. rufipileatus*, and *A. melanopezus* for qualitative comparison with the vocalizations of *A. infuscatus*. This involved both auditory comparison and superficial visual comparison of spectrograms. Locations and recordists for all recordings of *A. infuscatus* examined are given in Appendix 1. For comparison, vocalizations were categorized as loudsongs, calls, and long calls. Loudsongs were consistently patterned multinote vocalizations (Isler et al. 1997) given seemingly in the context of territorial advertisement. Vocalizations characterized as calls usually were structurally simple (typically involving well-spaced repetition of identical notes or pairs of notes), and most often were given in the context of contact notes between mates, or as aggression calls during territorial conflicts with conspecifics, or in response to tape playback. Exceptions are noted in the results, below. Vocalizations categorized as long calls were infrequently given series of mostly identical single note calls delivered in rapid succession, the context of which was unclear. My tape recordings were made with a Sony TCM-5000 recorder with Sennheiser ME-80 and MKH-70 shotgun microphones. Spectrograms used in illustrations were made by P. R. Isler on a Macintosh G4 computer using Canary version 1.2.1 (Bioacoustics Research Program, Cornell Lab. of Ornithology, Ithaca, New York), Canvas graphics software (version 5.0.3, Deneba Software, Miami, Florida), and a Hewlett Packard Laserjet 6MP printer.

To identify morphological differences, I examined representative specimens of *A. i. infuscatus* ($n = 83$), *A. i. purusianus* ($n = 40$), *A. i. paraensis* ($n = 83$), *A. i. badius* ($n = 57$), and *A. i. cervicalis* ($n = 39$). These specimens are housed at the Academy of Natural Sciences of Philadelphia, Philadelphia (ANSP); Carnegie Museum, Pittsburgh (CM); Field Museum of Natural History, Chicago (FMNH); Los Angeles County Museum of Natural History, Los Angeles (LACM); Louisiana State Univ. Museum of Natural Science, Baton Rouge (LSUMZ); National Museum of Natural History, Washington, D.C. (USNM); and the Peabody Museum of Natural History, Yale Univ., New Haven (YPM) (Appendix 2). A wing rule with a perpendicular stop at zero was used to measure wing chord (wing), tail length (tail), and hind toe length (hind toe), and dial calipers were used to measure tarsus length (tarsus), culmen length from the anterior end of the nares to the tip (culmen), bill depth at the anterior end of the nares (bill depth), bill width at the anterior end of the nares (bill width), and hind claw length (hind claw). All measurements made with calipers were to the nearest 0.1 mm; those taken with the wing rule were to the nearest 0.5 mm. Measurement terminology conforms with that used by Pyle et al. (1987). Plumage was described from specimens and compared to a standard color reference (Smithe 1975).

General linear models were used to investigate gender-corrected differences among the five subspecies for each of the eight characters measured. Residual diagnostics indicated no violations of the general linear model assumptions of error normality and constant variance. Bonferonni multiple comparisons (two-tailed *t*-test) with a family error rate of 5% were used to compare pairwise subspecies differences for each variable (Sokal and Rohlf 1995). Intervals that do not contain zero indicate a significant difference among the pair of species. Statistical analyses (ANOVA procedure and Bonferonni multicomp procedure) were performed using S-Plus version 4.5 for Windows.

RESULTS

Distribution.—Nominate *A. i. infuscatus* occurs in western Amazonia, from southeastern Colombia south through the lowlands of eastern Ecuador and eastern Peru to Bolivia (Fig. 1). *Automolus infuscatus purusianus* replaces nominate *infuscatus* in western Brazil south of the Solimães (= Amazon), east to the left

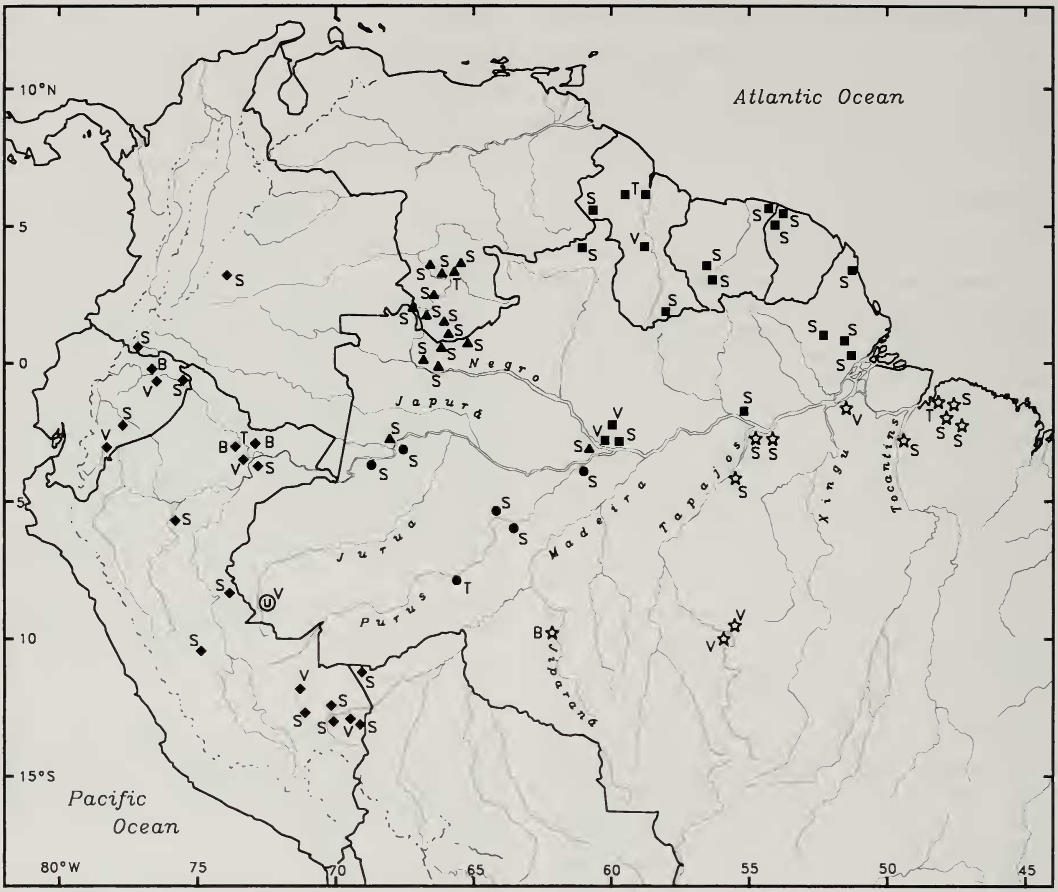


FIG. 1. Distribution of "Olive-backed" Foliage-gleaners (*Automolus infuscatus*) as confirmed by examination of specimens or tape recordings: open stars = *A. i. paraensis*; black diamonds = *A. i. infuscatus*; black circles = *A. i. purusianus*; black triangles = *A. i. badius*; black squares = *A. i. cervicalis*; "T" next to a symbol indicates the type locality for that taxon; "S" next to a symbol indicates specimen confirmation for that taxon; "V" next to a symbol indicates vocal confirmation (tape recording) for that taxon; "B" next to a symbol indicates both specimen and vocal confirmation for that taxon; and "U" in a circle locates Porongaba, Acre, Brazil, from which archived tape recordings could not be identified with certainty (either *A. i. infuscatus* or *A. i. purusianus*).

bank of the Rio Madeira. It probably contacts *A. i. infuscatus* in extreme western Brazil, possibly in the upper regions of the Rio Juruá or Purus, but this has yet to be determined. *Automolus i. paraensis* occurs south of the Amazon and east of the Rio Madeira to the right bank of the Rio Tocantins. North of the Amazon, the complex is represented by two subspecies: *A. i. badius*, from central edo. Bolívar, Venezuela west to the upper Rio Negro region of eastern Colombia and south through northwestern Brazil along the west bank of the Rio Negro to its mouth; and *A. i. cervicalis*, from northeastern edo. Bolívar, Venezuela east through French Guiana and in Brazil north of the Amazon and east of the Rio Negro through Amapá. These two north bank forms may contact one another in northern Brazil above the confluence of the Rio Branco and Rio Negro, but this has yet to be determined.

Habitat.—All forms of *A. infuscatus* are found in lowland humid forest below 1,000 m. They occur in *várzea*, transitional, and *terra firme* forest, but generally are more common in the latter habitat.

Behavior.—All forms of *A. infuscatus* occupied the lower to mid-levels of the forest strata, and usually were encountered as members of mixed species flocks of insectivores comprised primarily of woodcreepers, other foliage-gleaners, antshrikes (mainly *Thamnomanes* spp.) and antwrens (*Myrmotherula* spp.). My observations of *A. i. badius*, *A. i. cervicalis*, *A. i. infuscatus* and *A. i. paraensis* suggest they are all dead-leaf-searching specialists (>75% of all foraging maneuvers involved searches of dead leaves for arthropods), probing dead leaves suspended in vine tangles and in crowns of understory trees (particularly palms). During these searches, foliage-gleaners clung acrobatically (often upside down) onto palm fronds, vines, or large dead leaves (particularly those of *Cecropia* spp. and species of palms), and probed with their bill for 1–15 s into curled dead leaves. An individual would routinely hold large dead leaves steady with its foot and then tear the leaf apart with its bill, using a variety of hammering and shredding motions. Where mats of many dead leaves were trapped in a tangle or the crown of a palm, foliage-gleaners would use their bill to vigorously toss out one leaf after another in search of prey.

Plumage.—The five subspecies of Olive-backed Foliage-gleaner are so similar in plumage characters that silent birds could easily defy identification in the field. In direct comparison, specimens usually were separable by a combination of dorsal coloration, crown pattern, and the degree of contrast between the crown-nape and back. *Automolus i. badius* is distinctly more reddish dorsally than all other subspecies, the back being between Raw Umber (color #223, capitalized color names from Smithe 1975) and Proutãs Brown (color #121A). The crown and nape feathers have minimally contrasting darker fringes, lending a slight scaly pattern, but the ground color of the crown and nape is uniform with the back. The other subspecies are more truly "olive-backed," with *A. i. infuscatus*, *A. i. paraensis*, and *A. i. cervicalis* all having the back closest to Dark Brownish Olive (color #129), and *A. i. purusianus* being close to this color but perhaps marginally more reddish (closest to Hair Brown, color #119A). Of these forms, *A. i. paraensis* is the most distinctly plumaged. The feathers of the crown and nape are noticeably grayer, contrasting with the brownish olive back. These feathers also have fairly broad dark terminal fringes, which creates a distinct scaly pattern to the crown and nape. Nominate *infuscatus* also has dark terminal fringes to the crown and nape feathers, but the feather centers are brownish olive like those of the back (not distinctly grayer as in *A. i. paraensis*), and the terminal fringes are narrower, with the result that there is less contrast between the nape and back. *Automolus i. purusianus* has much less distinct dark fringing to the crown and nape feathers, and the overall effect is of the crown, nape, and back being uniformly colored (as in *A. i. badius* but less reddish). *Automolus i. cervicalis* has even less dark fringing to the crown and nape feathers, but these are a warmer brown color than the back, and thus, contrast slightly.

All five subspecies have rufescent tails which contrast with the drab upperparts. The contrast is least conspicuous in *A. i. badius*, which is distinctly more reddish dorsally than the other forms. *Automolus i. paraensis* has the tail a deeper rust color than the other forms, the color being between Burnt Sienna (color #132) and Mars Brown (color #223A). All subspecies are similar ventrally, being dingy grayish-buff, with browner flanks and a contrasting creamy-white throat. The only exception is *A. i. badius*, which, although generally similar, is distinctly grayer from the midbreast to the belly.

Size.—Subspecies of *Automolus infuscatus* differed from one another in mean measurements of all characters that were measured (Tables 1, 2; Fig. 2). Between-taxa differences were found in measurements of culmen ($F_{4,284} = 13.3$, $P < 0.0001$), bill depth ($F_{4,279} = 6.6$, $P = 0.0001$), bill width ($F_{4,287} = 3.1$, $P = 0.015$), wing chord ($F_{4,287} = 21.8$, $P < 0.0001$), tail length ($F_{4,285} = 14.3$, $P < 0.0001$), tarsus ($F_{4,285} = 44.6$, $P < 0.0001$), hind claw ($F_{4,285} = 49.3$, $P < 0.0001$), and hind toe ($F_{4,286} = 48.7$, $P < 0.0001$). There were no biometric differences between *A. i. infuscatus* and *A. i. paraensis* (Table 2). *Automolus i. paraensis* and *A. i. infuscatus* differed from *A. i. purusianus* only in wing chord. *Automolus i. badius* and *A. i. cervicalis* differed from one another in culmen length, wing chord, and hind claw length. All other differences reflected a split between smaller taxa from north of the Amazon (*A. i. badius* and *A. i. cervicalis*), and larger taxa whose ranges were predominantly or entirely south

TABLE 1. Means (± SD), ranges, and sample sizes of selected measurements (mm) of the five subspecies of Olive-backed Foliage-gleaner (*Automolus infuscatus*). Significance: * = $P < 0.001$; ** = $P < 0.0001$. Values of F and P are from ANOVA. Asterisks following a character indicate differences between two or more of the subspecies, after correcting for potential sex differences within taxa.

Characters	*badius*	*cervicalis*	*infuscatus*	*paraensis*	*purusianus*	*F*
Culmen**	14.1 ± 0.6	13.6 ± 0.6	14.2 ± 0.7	14.5 ± 0.7	14.3 ± 0.7	13.3
	12.9–15.6	11.8–15.2	12.5–16.2	13.1–16.6	12.9–15.9	
	($n = 50$)	($n = 37$)	($n = 82$)	($n = 83$)	($n = 39$)	
Bill depth**	6.5 ± 0.3	6.6 ± 0.3	6.6 ± 0.3	6.7 ± 0.3	6.7 ± 0.3	6.6
	6.0–7.1	6.1–7.1	6.0–7.2	5.9–7.3	6.1–7.4	
	($n = 51$)	($n = 35$)	($n = 81$)	($n = 80$)	($n = 39$)	
Bill width*	5.0 ± 0.2	5.1 ± 0.2	5.2 ± 0.2	5.2 ± 0.2	5.1 ± 0.3	3.1
	4.4–5.6	4.7–5.6	4.7–5.7	4.7–5.7	4.3–5.6	
	($n = 52$)	($n = 37$)	($n = 82$)	($n = 83$)	($n = 40$)	
Wing chord**	89.0 ± 3.4	86.3 ± 3.1	90.6 ± 3.7	89.8 ± 3.7	93.1 ± 3.6	21.8
	80.5–95.5	77.5–91	83–98.5	82–97	84.5–100	
	($n = 52$)	($n = 37$)	($n = 82$)	($n = 83$)	($n = 40$)	
Tail**	75.0 ± 3.2	75.2 ± 4.0	78.1 ± 4.1	79.1 ± 3.5	78.1 ± 4.2	14.3
	68–82.5	68–85	70–88.5	72–87	71–91	
	($n = 52$)	($n = 37$)	($n = 82$)	($n = 81$)	($n = 40$)	
Tarsus**	21.7 ± 0.8	21.6 ± 0.9	22.8 ± 0.8	23.1 ± 0.7	23.0 ± 1.0	44.6
	20.5–23.8	20–23.8	20.3–24.5	21.1–25.5	20.3–25	
	($n = 52$)	($n = 37$)	($n = 82$)	($n = 82$)	($n = 39$)	
Hind claw*	7.0 ± 0.3	6.7 ± 0.4	7.5 ± 0.4	7.4 ± 0.3	7.5 ± 0.4	49.3
	6.4–7.6	5.8–7.6	6.5–8.5	6.7–8.1	6.6–8.6	
	($n = 52$)	($n = 37$)	($n = 82$)	($n = 82$)	($n = 39$)	
Hind toe**	10.4 ± 0.5	10.2 ± 0.6	11.3 ± 0.6	11.2 ± 0.5	11.3 ± 0.6	48.7
	9.5–11.5	9–11	10–12.5	10–13	10–12.5	
	($n = 52$)	($n = 37$)	($n = 82$)	($n = 82$)	($n = 40$)	

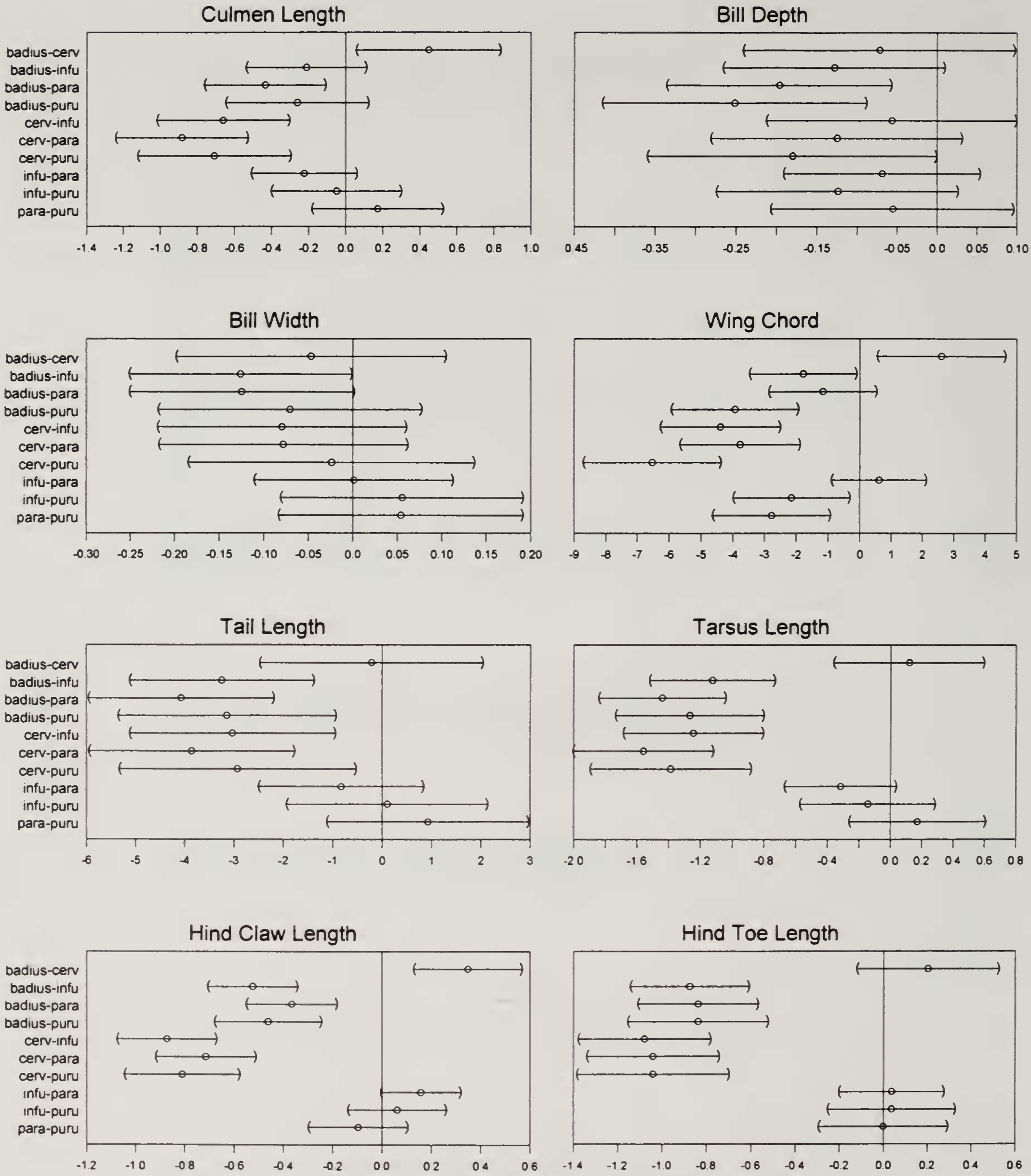
of the Amazon (*A. i. infuscatus*, *A. i. purusianus*, and *A. i. paraensis*). In spite of mean differences between taxa, ranges for each of the variables were overlapping, and no taxon could be diagnosed solely on biometric characters (Fig. 2).

Vocalizations.—I assembled recordings of 98 different Olive-backed Foliage-gleaners (55 *A. i. infuscatus*, 30 *A. i. paraensis*, eight *A. i. cervicalis*, three *A. i. badius*, two taxon unidentified), including more than 900 individual songs and 1,100 calls. All subspecies except *A. i. purusianus* were represented.

Spectrographic analysis confirmed my field impressions that *A. i. paraensis* differed strikingly and consistently in all aspects of its vocal repertoire from all other subspecies in the complex. The loudsong of this subspecies (Fig. 3A–D) was a loud series of 2–17 well-spaced, frequency-modulated notes, each of which had a particularly harsh, grating quality. The number of notes and the length of songs varied within a song bout in the same individual. Typical songs contained 4–10 notes (85.2% of all songs; 57% of all songs composed of ≤ 6 notes) and began with a differentiated note that was longer than all subsequent notes in the song (*jureet-reetreetreetreet* or *breek brik brik brik brik*). Individuals occasionally sang longer songs (Fig. 3C) of 11–17 notes (14.8% of all songs recorded), that began with a less differentiated first note followed by a longer than average interval before the next note, and were then evenly paced through the remainder of the song. These songs give the impression of a grating laugh. Within a song bout, individuals tended to sing 4–5 consecutive songs with an identical number of notes before adding or subtracting notes. When presented with tape playback of short songs (3–6 notes), birds usually responded with distinctly longer songs, but when presented with tape playback of longer songs (≥ 10 notes) they usually reverted to short songs. Both short and long responses to playback fell within the same range of notes found in natural (unsolicited) songs. The most common call was a loud, single-noted *quip* or

TABLE 2. Bonferroni multiple comparisons of eight biometric variables (mm) between the five subspecies of Olive-backed Foliage-gleaner (*Automolus infuscatus*). All measurements are from museum specimens. For each intertaxon comparison, the t-values are listed above the associated values of P. Degrees of freedom for t-values = 284 (culmen), 279 (bill depth), 287 (bill width, wing chord), 285 (tail, tarsus, hind claw), and 286 (hind toe). Differences between taxa are considered significant (*) only when $P < 0.005$, to achieve a Bonferroni family error rate of 0.05.

	Culmen	Bill depth	Bill width	Wing	Tail	Tarsus	Claw	Toe
badius-cervicalis	3.27	−1.20	−0.87	3.63	−0.27	0.71	4.54	1.80
	0.001*	0.230	0.383	0.000*	0.787	0.479	0.000*	0.073
badius-infuscatus	−1.87	−2.64	−2.86	−3.02	−4.93	−8.19	−8.26	−9.36
	0.063	0.009	0.004*	0.003*	0.000*	0.000*	0.000*	0.000*
badius-paraensis	−3.80	−4.01	−2.81	−1.95	−6.15	−10.29	−5.69	−8.84
	0.002*	0.000*	0.005	0.053	0.000*	0.000*	0.000*	0.000*
badius-purusianus	−1.93	−4.36	−1.35	−5.62	−4.05	−7.74	−6.11	−7.54
	0.055	0.000*	0.178	0.000*	0.000*	0.000*	0.000*	0.000*
cervicalis-infuscatus	−5.27	−1.02	−1.61	−6.66	−4.13	−8.00	−12.33	−10.29
	0.000*	0.307	0.108	0.000*	0.000*	0.000*	0.000*	0.000*
cervicalis-paraensis	−7.05	−2.28	−1.58	−5.70	−5.25	−10.07	−10.07	−9.90
	0.000*	0.024	0.114	0.000*	0.000*	0.000*	0.000*	0.000*
cervicalis-purusianus	−4.88	−2.85	−0.42	−8.60	−3.46	−7.81	−9.88	−8.67
	0.000*	0.004*	0.677	0.000*	0.000*	0.000*	0.000*	0.000*
infuscatus-paraensis	−2.22	−1.58	0.04	1.19	−1.41	−2.54	2.79	0.46
	0.027	0.114	0.970	0.236	0.159	0.012	0.006	0.649
infuscatus-purusianus	−0.40	−2.35	1.16	−3.35	0.14	−0.95	0.89	0.37
	0.692	0.020	0.247	0.001*	0.886	0.344	0.375	0.712
paraensis-purusianus	1.40	−1.04	1.12	−4.27	1.29	1.14	−1.37	−0.004
	0.161	0.301	0.262	0.000*	0.196	0.256	0.171	0.997


Culmen Length

Bill Depth

Bill Width

Wing Chord

Tail Length

Tarsus Length

Hind Claw Length

Hind Toe Length

FIG. 2. Graphical display of Bonferonni multiple comparisons of eight biometric variables (as measured from museum specimens) between the five subspecies of Olive-backed Foliage-gleaner (*Automolus infuscatus*). Test values are in Table 2. Codes for the taxa are: badius = *A. i. badius*; cerv = *A. i. cervicalis*; infu = *A. i. infuscatus*; para = *A. i. paraensis*; puru = *A. i. purusianus*. Intervals that do not contain zero indicate a significant difference among the pair of subspecies being compared.

queep, with a distinctly liquid quality (Fig. 3E, F). Less frequently given was a similar sounding two-noted call in which the first and second notes were slightly differentiated (Fig. 3G). These two calls were given as contact calls by both members of a foraging pair, but also were delivered in an aggressive context in response to tape playback or the presence of neighboring conspecifics. The long call was a series of 4–10 *quip* notes that accelerated

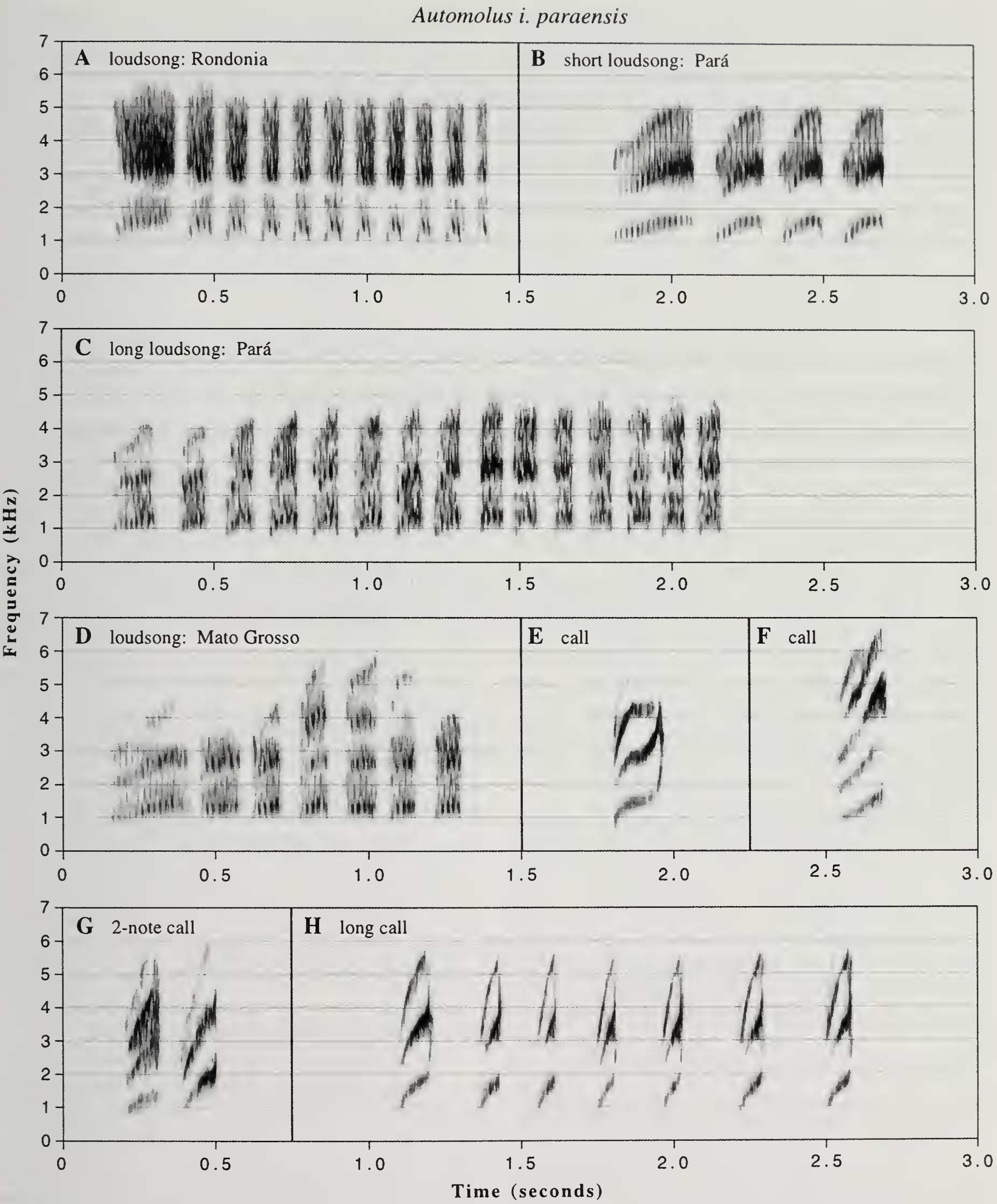


FIG. 3. Types of vocalizations of *Automolus infuscatus paraensis*: (A) loudsong from Rondônia, Brazil (T. S. Schulenberg recording, LNS #43362); (B) short loudsong from Pará, Brazil; (C) long loudsong from Pará, Brazil; (D) loudsong from Mato Grosso, Brazil; (E) *queep* call from Pará, Brazil; (F) *queep* call from Mato Grosso, Brazil; (G) two-note call from Mato Grosso, Brazil; and (H) long call from Mato Grosso, Brazil. Except as noted, all recordings by K. J. Zimmer.

after the initial note and then slowed toward the end (Fig. 3H). Birds from Rondônia, Mato Grosso, and Pará were similar in all vocalizations. Variations in songs (Fig. 3) are indicative of variations between songs of a single individual, as well as of variations among individuals of a single population. They do not reflect any consistent geographic variation that I could identify.

In contrast, the loudsongs of *A. i. infuscatus*, *A. i. cervicalis*, and *A. i. badius* were slightly descending rattles that were similar to one another in pattern and pitch, but differed in length (Fig. 4). The rattle of each subspecies was an evenly paced series of rapidly delivered similar notes that began at about 4 kHz and leveled off at about 3 kHz. The loudsongs of each of these three subspecies were similarly paced, and were delivered at a rate too fast for the human ear to clearly distinguish individual notes. The loudsongs of *A. i. infuscatus* (Fig. 4A–C) averaged about twice as many notes as those of *A. i. cervicalis* (Fig. 4D–F) and *A. i. badius* (Fig. 4G). There were no appreciable differences between the songs of the latter two subspecies, nor was there evidence of consistent geographic variation in the songs of either *A. i. infuscatus* or *A. i. cervicalis*.

The calls of *A. i. infuscatus*, *A. i. badius*, and *A. i. cervicalis* also were highly differentiated from those of *A. i. paraensis*. The most commonly heard call from *A. i. infuscatus* is a two-noted *chik-uh* or *chik-it* in which the first note is higher pitched than the second (Fig. 5A, B). This call frequently was given by both members of a foraging pair, and functioned as a contact call or a heightened awareness call. It also was delivered repeatedly by birds responding to tape playback. Nominate birds also gave a sharp, squeaky, single-noted call that was similar to the first note of the two-noted call (Fig. 5C, D), as well as a hard rattle call that was similar to an abbreviated, flatter version of the loudsong (Fig. 5E). This latter vocalization was given most often in an aggressive context, particularly when birds responded to tape playback. The single-noted call is similar to the alarm squeaks given by the various species of leaftossers (*Sclerurus* spp.). The long call of nominate birds (Fig. 5F) begins with a differentiated, drawn out first note, followed by a series of ≥5 shorter identical notes given in rapid succession (*skeew wekwekwekwekwek*). Populations of nominate *infuscatus* from Ecuador, Peru, and Bolivia had similar calls.

The most frequently given calls of both *A. i. badius* and *A. i. cervicalis* (Fig. 5G, H) were two-noted, with the first note being shorter and higher-pitched (*chik-qwaah*). This call is markedly similar to the primary songs of some spinetails of the genus *Synallaxis*. It is somewhat similar to the two-noted call of *A. i. infuscatus* (Fig. 5A, B), but differs in being slower, with the two notes more strongly differentiated from one another. Differences in tonal quality between the two-noted calls of nominate birds and those of *A. i. badius* and *A. i. cervicalis* are reflected in the obvious differences in note shape as seen in the spectrograms. Single-note *chik* or *stit* calls (Fig. 5I) of the latter two subspecies also were similar, and differed from those of nominate birds in being less squeaky sounding. As was true with *A. i. infuscatus*, the two-note and one-note calls of *A. i. badius* and *A. i. cervicalis* appeared to function as contact calls between mates, as heightened awareness calls when birds were alarmed by my presence, and as aggression calls when birds were responding to tape playback. Two additional calls were noted for *A. i. badius*: a harsh *chek* (Fig. 5J); and a harsh, downslurred *cheer* (Fig. 5K). The small samples of *A. i. badius* and *A. i. cervicalis* recordings did not include long calls, nor did I note such calls in the field. Whether this reflected an absence of such a vocalization type from the repertoires of the two north bank forms, or was merely an artifact of sampling error, has yet to be determined.

A recording of a pair of birds from the upper Rio Juruá (Porongaba, Acre, Brazil) may be of *A. i. purusianus*, but the subspecific identity of Olive-backed Foliage-gleaners from that region is uncertain. The recorded vocalizations, which include songs, single-note calls, and two-note calls, are indistinguishable from those of nominate *A. infuscatus*.

Plumage, biometric, and vocal characters distinguishing the five subspecies are summarized in Fig. 6.

DISCUSSION

Spectrographic comparison of vocal characters reveals that Olive-backed Foliage-

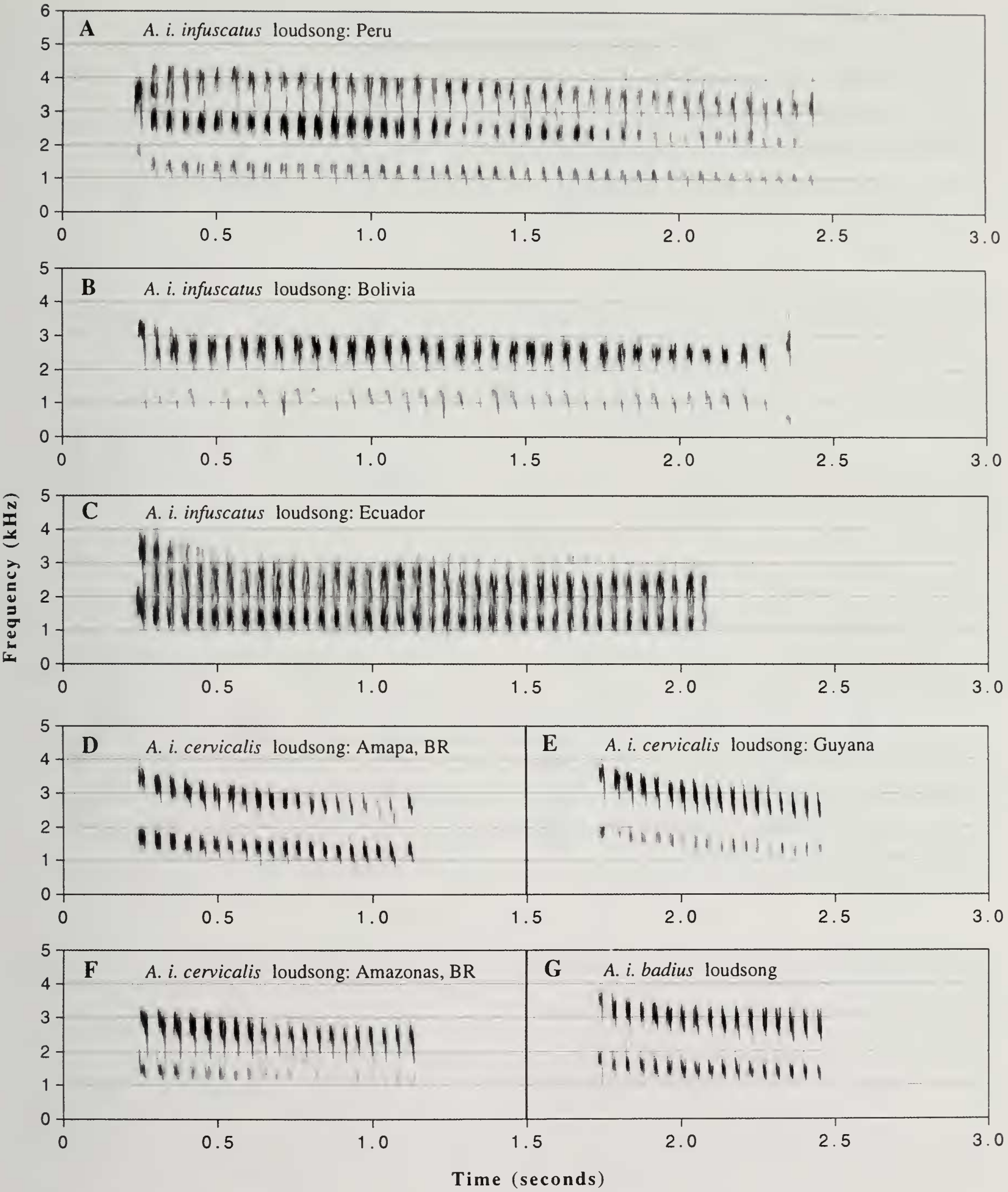


FIG. 4. Loudsongs of subspecies of *Automolus infuscatus*: (A) *A. i. infuscatus* from Loreto, Peru (T. A. Parker recording, LNS #29335); (B) *A. i. infuscatus* from Pando, Bolivia (T. A. Parker recording, LNS #38893); (C) *A. i. infuscatus* from Napo, Ecuador (K. J. Zimmer recording); (D) *A. i. cervicalis* from Amapá, Brazil (K. J. Zimmer recording); (E) *A. i. cervicalis* from Guyana (R. S. Ridgely recording); (F) *A. i. cervicalis* from Amazonas, Brazil (M. Cohn-Haft recording, LNS #48574); and (G) *A. i. badius* from Amazonas, Brazil (K. J. Zimmer recording).

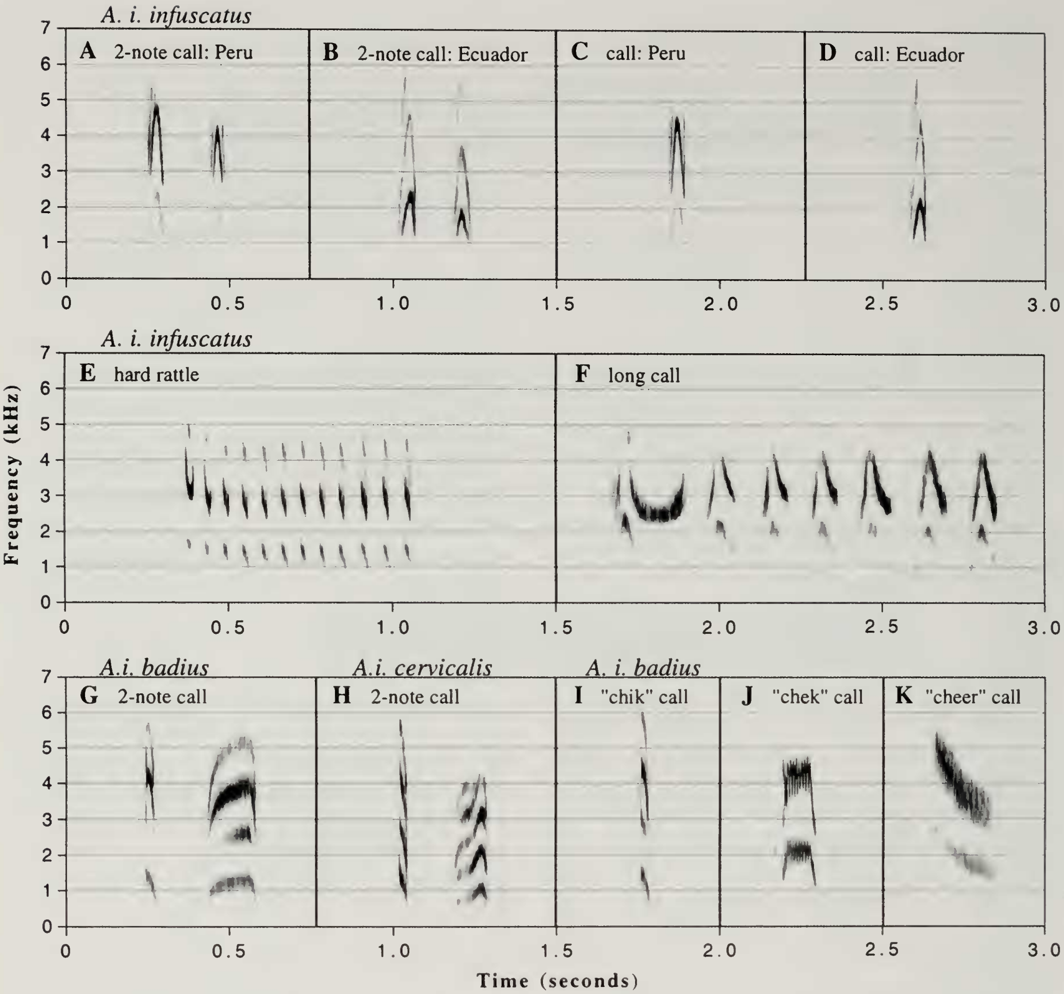


FIG. 5. Types of calls of subspecies of *Automolus infuscatus*: (A) two-note call of *A. i. infuscatus* from Madre de Dios, Peru (T. A. Parker recording, LNS #24224); (B) two-note call of *A. i. infuscatus* from Napo, Ecuador (K. J. Zimmer recording); (C) single-note call of *A. i. infuscatus* from Madre de Dios, Peru (T. A. Parker recording, LNS #23955); (D) single-note call of *A. i. infuscatus* from Napo, Ecuador (K. J. Zimmer recording); (E) hard rattle call of *A. i. infuscatus* from Madre de Dios, Peru (T. A. Parker recording, LNS #24123); (F) long call of *A. i. infuscatus* from Loreto, Peru (T. A. Parker recording, LNS #30724); (G) *chik-qwaah* call of *A. i. badius* from Amazonas, Brazil (K. J. Zimmer recording); (H) *chik-qwaah* call of *A. i. cervicalis* from Amazonas, Brazil (M. Cohn-Haft recording, LNS #48574); (I) *chik* call of *A. i. badius* from Amazonas, Brazil (K. J. Zimmer recording); (J) *chek* call of *A. i. badius* from Amazonas, Brazil (K. J. Zimmer recording); and (K) *cheer* call of *A. i. badius* from Amazonas, Brazil (K. J. Zimmer recording).

gleaners from south of the Amazon and east of the Rio Madeira (= *A. i. paraensis*) differ dramatically in their vocalizations from all other populations in the complex (Figs. 3–5). The loudsongs of *A. i. paraensis* differ in pattern, pace, pitch, tonal quality, and in individual note shape from the loudsongs of any other populations. Their calls (both single-noted and two-noted) and long calls are equally distinct from the corresponding vocalizations of any other subspecies.

The vocal distinctions between *A. i. paraensis* and other Olive-backed Foliage-gleaners are even more noteworthy when the lack of intrataxon variation within the complex is considered. Tape recordings of nominate *A. i. infuscatus* from Ecuador, Peru, and Bolivia show no striking geographic differences in

	paraensis	***infuscatus***	***purusianus***	***cervicalis***	***badius***
Size	Large	Large	Large	Small	Small
Back color	Dark brownish-olive	Dark brownish-olive	Hair brown	Dark brownish-olive	Raw Umber/ Prout's Brown
Crown/Nape color	Grayer than back	Same as back	Same as back	Warmer brown than back	Same as back
Crown scaling	Distinct	Indistinct	Indistinct	Indistinct	Indistinct
Color of breast/belly	Dingy gray-buff	Dingy gray-buff	Dingy gray-buff	Dingy gray-buff	Grayer than other taxa
Song type	2–17 widely spaced notes	Long, descending rattle (> 35 notes)	Unknown	Short, descending rattle (< 25 notes)	Short, descending rattle (< 25 notes)
Note structure	Strongly modulated	Unmodulated	Unknown	Unmodulated	Unmodulated
Note length	Long	Short	Unknown	Short	Short
Two-note calls	Notes mildly differentiated & liquid	Notes mildly differentiated & sharp	Unknown	Notes strongly differentiated	Notes strongly differentiated

FIG. 6. A summary of plumage, biometric, and vocal characters distinguishing the five subspecies in the Olive-backed Foliage-gleaner (*Automolus infuscatus*) group. Capitalized color descriptions follow Smithe (1975). Measurement data are provided in Table 1.

loudsongs or calls (Figs. 4, 5). Similarly, loudsongs of *A. i. cervicalis* do not vary from Manaus, Brazil to Amapá or Guyana, nor do they appear to differ from recordings of *A. i. badius* from west of the Rio Negro (Fig. 4).

Apart from the highly differentiated vocalizations of *A. i. paraensis*, there is further vocal variation within the complex to consider. The songs and calls of *A. i. infuscatus*, *A. i. badius*, and *A. i. cervicalis* all are far more similar to one another than any of them are to *A. i. paraensis*. However, the songs of the two north bank forms are only half as long as those of nominate *infuscatus* (Fig. 4), and at least some of the calls of both *A. i. badius* and *A. i. cervicalis* would appear to be diagnosably different as well (Fig. 5).

Morphological variation corresponds to some of the divisions suggested by vocal characters. Biometrically, the three southern forms (*A. i. infuscatus*, *A. i. purusianus*, and *A. i. paraensis*) are larger in most measured characters than are the two northern forms (*A. i. badius* and *A. i. cervicalis*). *Automolus i. badius* averaged smaller than each of the three southern forms in six of the eight characters measured. Similarly, *A. i. cervicalis* averaged smaller than *A. i. infuscatus* and *A. i. paraensis* in six characters, and differed from *A. i. purusianus* in seven characters. The three southern subspecies were poorly differentiated from one another biometrically. *Automolus i. infuscatus* and *A. i. paraensis* showed no differences over the eight mensural characters that I examined, and each differed from *A. i. purusianus* only in wing chord. The northern subspecies differed from one another in only three of the eight characters.

Plumage distinctions, although subtle, were consistent for each of the subspecies, and showed some trends that follow the north-south division in biometric differences. The smaller, northern subspecies were generally browner dorsally with only a slight dark scaling pattern to the crown and nape feathers. This was particularly true of *A. i. badius*, which was uniformly reddish-brown above. *Automolus i. cervicalis*, although more olivaceous on the back than *A. i. badius*, was still distinctly browner on the crown and nape than were the southern subspecies. This agrees with Hellmayr (1925:213), who stated that *A. i. cervicalis* was "similar to *A. i. infuscatus*, but crown and hindneck decidedly rufescent, more or less contrasting with olive brown of back, and flanks generally more brownish." Of the larger, southern subspecies, two (*A. i. infuscatus* and *A. i. paraensis*) were generally drab and more olivaceous dorsally, with a more pronounced pattern of dark scaling on the crown and nape. The contrasting gray crown and nape of *A. i. paraensis* were cited by Hartert (1902:61) in his description of the subspecies, and also were noted, along with the drabber coloration of the upperparts, by Hellmayr (1925:214) in his review of the complex.

The extremes of morphological variation within the complex are found in a comparison of *A. i. badius* (small; distinctly reddish-brown back; nape and crown concolor with the back; slight dark scaling to crown and nape; distinctly grayish underparts) and *A. i. paraensis* (large; back color olive; nape and crown contrastingly grayer than back; crown and nape feathers with distinctly scaly pattern; underparts dingy buff). These two forms are divergent enough that, in the absence of other populations, they could be considered specifically distinct on morphological grounds alone. However, unless vocal characters are considered, none of the other named subspecies is sufficiently different morphologically from both *A. i. badius* and *A. i. paraensis* to justify recognition of more than one species, at least under a biological species concept.

Spectrographic and auditory comparison of vocal characters throughout the genus suggests that *A. i. paraensis* may be more closely related to the subspecies of White-eyed Foliage-gleaner (*A. leucophthalamus*) in northeast Brazil (*A. l. lammi*), than it is to any other subspecies of *A. infuscatus*. The loudsongs of *A. i. paraensis* are more similar in pitch, pace, pattern, and note shape to those of *A. l. lammi* (Fig. 7A) than they are to those of any other member of the *A. infuscatus* complex. The loudsongs of *A. i. paraensis* and *A. l. lammi*, although different in several characters, are markedly similar to one another in their frequency-modulated, strident quality, a character that is not shared with any other taxon in the genus (KJZ recordings). The two-noted call of *A. l. lammi* (Fig. 7B) also is closer to that of *A. i. paraensis* than are the corresponding calls of nominate *A. infuscatus* (Fig. 5A,

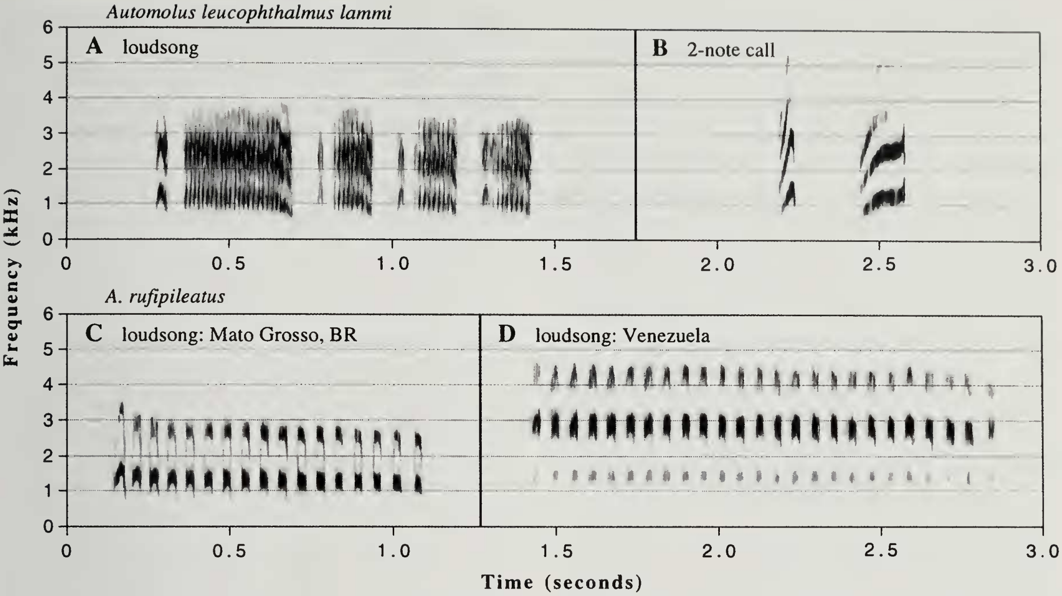


FIG. 7. (A) loudsong of *Automolus leucophthalamus lammi* from Sergipe, Brazil; (B) two-note call of *A. l. lammi* from Sergipe, Brazil; (C) loudsong of *A. rufipileatus* from Mato Grosso, Brazil; and (D) loudsong of *A. rufipileatus* from Bolívar, Venezuela (K. J. Zimmer recordings).

B). Willis (1988) suggested a possible superspecies relationship between *A. infuscatus* and *A. leucophthalamus* based on certain vocal similarities, but did not elaborate. On the basis of morphological characters, Vaurie (1980) also treated *A. infuscatus* and *A. leucophthalamus* as being more closely related to one another than to other members of the genus. However, it also should be noted that the same analysis of morphological characters (in the absence of vocal characters) led Vaurie (1980) to include *Automolus dorsalis* (now = *Anabazenops dorsalis*; Kratter and Parker 1997) in the same superspecies grouping with *A. infuscatus* and *A. leucophthalamus*. The relationship of *A. l. lammi* to other members of the *A. leucophthalamus* complex will be considered in a separate paper.

The distribution of *A. i. paraensis* as a species level taxon distinct from other members of the complex makes sense biogeographically. There is a well-documented pattern of species replacement within genera across both the Amazon and the Madeira (Haffer 1992). The distribution of *A. i. paraensis* overlaps three proposed centers of avian endemism as defined by Cracraft (1985): the Rondônia Center, delimited by the Rio Madeira and Rio Beni to the west, the Amazon to the north, the limit of tropical humid forest to the south, and the Rio Tapajós (in some cases, the Rio Xingú) to the east; the Pará Center, delimited by the Rio Tapajós to the west, the Amazon to the north, the limit of tropical humid forest to the south, and the Rio Tocantins to the east; and the Belém Center, which extends from the Rio Tocantins on the west, north to the Amazon, east to the Atlantic Coast, and south to the limit of the tropical humid forest. Numerous species of birds are endemic to all or part of the range occupied by *A. i. paraensis* (Cracraft 1985).

Recent studies of Neotropical suboscine passerines have revealed numerous cases of cryptic biodiversity, in which distinct species level taxa with dramatically different vocalizations were long overlooked because of their morphological similarity to more widespread forms (e.g., Pierpont and Fitzpatrick 1983; Willis 1992; Bierregaard et al. 1997; Zimmer and Whittaker 2000a, 2000b; Zimmer et al. 2001). As access to behavioral, ecological, vocal, and molecular data increases, it is becoming clear that taxonomies based solely on morphological distinctions severely underestimate species level biodiversity. Olive-backed Foliage-gleaners provide yet another example.

TAXONOMIC CONCLUSIONS

Automolus infuscatus paraensis differs substantially in every known vocal character from all other subspecies in the complex. It also differs morphologically from all other members of the group, although these distinctions are more subtle. In particular, it can be separated from all other Olive-backed Foliage-gleaners by the contrasting grayish crown and nape, with broader, more contrasting dark fringes to the individual feathers. It is further differentiated from the two northern subspecies by its larger size, and lack of brown coloration on the crown or back.

The extent of the vocal differences alone is more than sufficient to support the recognition of *A. i. paraensis* as a separate species under any of the widely accepted species concepts (McKitrick and Zink 1988). Because *A. i. paraensis* is allopatrically or parapatrically distributed with respect to the other members of the complex, the most difficult species concept to satisfy is the biological species concept. A primary challenge in applying the biological species concept to allopatrically distributed taxa is the need to judge whether or not the taxa are sufficiently differentiated as to prevent extensive hybridization in the event of secondary contact. Johnson et al. (1999) advocated using the degree of differentiation shown between accepted biological species in the same genus as a yardstick for assessing whether a taxon has diverged sufficiently to be considered a separate species under the Biological Species Concept (BSC). The Chestnut-crowned Foliage-gleaner (*A. rufipileatus*) is broadly sympatric with all of the subspecies of Olive-backed Foliage-gleaners (Ridgely and Tudor 1994), and thus provides an appropriate yardstick for comparison of species level vocal divergence within the genus. Loudsongs of *A. rufipileatus* from north and south of the Amazon (Fig. 7C, D) are far more similar to those of all other members of the *A. infuscatus* complex, excluding *paraensis*, (Fig. 4) than are loudsongs of *A. i. paraensis*. Spectrographic and auditory comparison reveals that the vocal differences between *A. i. paraensis* and all other subspecies in the *Automolus infuscatus* complex are as great or greater than between those subspecies and any congener outside of the complex. This would suggest that the vocal differences alone present effective mechanisms for reproductive isolation between *A. i. paraensis* and any other member of the group.

The relationships of the other subspecies in the complex are less obvious. It is tempting to recognize the two northern subspecies, *A. i. badius* and *A. i. cervicalis*, as a species distinct from the more southern *A. i. infuscatus* and *A. i. purusianus*. The northern birds are distinctly smaller, and differ in certain plumage characters. More importantly, they differ in several vocal characters from nominate *A. infuscatus*, although the differences are less obvious than those found in *A. i. paraensis*. The two groups (northern versus southern) would certainly meet phylogenetic species concept (PSC) criteria for diagnosability as separate species, and they may ultimately prove to be distinct biological species as well. However, I believe that vocal differences among these groups are subtle enough to warrant a more rigorous quantitative vocal analysis, and current sample sizes of the recording inventories for both *A. i. badius* ($n = 3$) and *A. i. cervicalis* ($n = 8$, but most recordings are of loudsongs without calls) are inadequate. Furthermore, it cannot be assumed that *A. i. purusianus*, for which there are no definite tape recordings, belongs with nominate *A. infuscatus*, solely because of morphological similarity. In the absence of any data on the vocalizations of *A. i. purusianus*, and lacking sufficient vocal samples of *A. i. badius* and *A. i. cervicalis*, I follow the conservative path of maintaining these forms, along with nominate *A. i. infuscatus*, as part of the *Automolus infuscatus* complex. I propose that the complex consists of two biological species as follows:

Automolus infuscatus Sclater—Olive-backed Foliage-gleaner
  A. i. infuscatus Sclater
  A. i. cervicalis Sclater
  A. i. badius Zimmer
  A. i. purusianus Todd
Automolus paraensis Hartert—Pará Foliage-gleaner

The English name chosen for *A. paraensis* highlights the Brazilian state which encompasses the bulk of its range, and from which the majority of specimens, including the type, have been collected. I have chosen to retain "Olive-backed Foliage-gleaner" as the English name for all other members of the complex. Should the two northern taxa prove to be specifically distinct from the two southern taxa, then the prefix "Olive-backed" would most appropriately be applied to the southern birds.

ACKNOWLEDGMENTS

Special thanks are due M. L. and P. R. Isler for lending their time and talents in producing the map and spectrograms (respectively) for this paper. K. L. Garrett, K. C. Molina and the staff at LACM were of inestimable help in coordinating specimen loans from various institutions, as well as logistical support for the author's frequent museum visits. T. S. Schulenberg was always available with helpful advice, and also provided access to several key references. Thanks also are due J. V. Remsen and S. W. Cardiff (LSUMZ); J. M. Bates, S. J. Hackett, T. S. Schulenberg, and D. E. Willard (FMNH); K. C. Parkes and R. K. Panza (CM); F. C. Sibley (YPM); S. L. Olson and P. Angle (USNM); and R. S. Ridgely and D. Agro (ANSP) for arranging specimen loans from their respective institutions. G. F. Budney, A. Priori, and the rest of the staff at the Library of Natural Sounds, Cornell Lab. of Ornithology were of great help in providing access to the LNS collection of recordings. R. A. Behrstock, M. B. Robbins, G. H. Rosenberg, and A. Whittaker generously provided additional tape recordings to add to my inventory. A. Schaffner provided valuable assistance with the statistical analysis of morphological data. Thanks to A. W. Kratter, J. V. Remsen, and an anonymous reviewer for their many helpful comments on this manuscript. Special thanks go to Victor Emanuel Nature Tours, Inc., for providing me with many of the travel opportunities that made this research possible. Finally, this paper is dedicated to the memory of my major professor, R. J. Raitt, whose guidance, encouragement, and informed insights into avian ecology I shall always remember.

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APPENDIX 1

Recording locations and recordists. Numbers following each name represent the number of individual birds recorded by the recordist at each site.

A. i. paraensis.—BRAZIL: Alta Floresta region, Mato Grosso (K. J. Zimmer 20); Caxiuanã Forest Reserve, Pará (K. J. Zimmer 9); Cachoeira Nazaré, Rondônia (T. S. Schulenberg 1).

A. i. infuscatus.—BOLIVIA: Suarez, Pando (T. A. Parker 1). ECUADOR: La Selva Lodge, N bank Rio Napo, Napo (R. A. Behrstock 2, G. H. Rosenberg 1); Santiago, Morona-Santiago (M. B. Robbins 2); Tiputini Biodiversity Station, S bank Rio Napo, Napo (K. J. Zimmer 9). PERU: S bank Rio Napo, 80 km N of Iquitos, Loreto (T. A. Parker 2, G. H. Rosenberg 1); Quebrada Sucusari, N bank Rio Napo, Loreto (T. A. Parker 6); Yanamono, N bank Rio Napo, Loreto (G. H. Rosenberg 2); Cocha Cashu, Manu National Park, Madre de Dios (T. A. Parker 1); Tambopata Reserve, Madre de Dios (M. L. Isler 1, L. Kibler 3, M. Palmer 2, T. A. Parker 16, G. A. Rosenberg 1, A. Van den Berg 4, K. J. Zimmer 1).

A. i. cervicalis.—BRAZIL: Serra do Navio, Amapá (K. J. Zimmer 1); left bank Rio Negro north of Manaus, Amazonas (M. Cohn-Haft 1, A. Whittaker 1). GUYANA: Baramita (M. B. Robbins 1); Iwokrama Reserve (R. S. Ridgely 1, M. B. Robbins 2); Waruma River (M. B. Robbins 1).

A. i. badius.—BRAZIL: São Gabriel da Cachoeira, Amazonas (right bank Rio Negro) (K. J. Zimmer 3).

A. i. purusianus or A. i. infuscatus.—BRAZIL: Porongaba, Acre (A. Whittaker 2).

APPENDIX 2

List of localities and lending institutions for specimens examined. All specimens were from the following institutions: Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania (ANSP); Carnegie Museum, Pittsburgh, Pennsylvania (CM); Field Museum of Natural History, Chicago, Illinois (FMNH); Los Angeles County Museum, Los Angeles, California (LACM); Louisiana State Univ. Museum of Natural Science, Baton Rouge, Louisiana (LSUMZ); National Museum of Natural History, Washington, D.C. (USNM); and the Yale Peabody Museum of Natural History, New Haven, Connecticut (YPM).

A. i. paraensis (46 males, 31 females, 5 sex unknown).—BRAZIL: Bela Vista, Pará (CM, 1 female); Belém, Pará (FMNH, 1 female; USNM, 10 males, 7 females, 5 sex unknown); Belém-Brasilia Rd. Km 75–107, Pará (LACM, 8 males, 2 females; LSUMZ, 3 males); Benevides, Pará (CM, 4 males, 4 females; YPM, 2 males, 1 female); Benfica, Pará (FMNH, 1 female); Cachoeira Nazaré, Rondônia (FMNH, 1 male); Colônia do Mojuy, Pará (CM, 8 males, 2 females; FMNH, 1 male, 1 female; YPM, 1 male); Lago do Araipa, Pará (LACM, 3 females); Mirituba, Pará

(CM, 2 males, 3 females; YPM, 1 male, 1 female); Pedra Branca, Rio Anari, Rondônia (FMNH, 2 males, 1 female); Santarém, Pará (CM, 2 males, 2 females; YPM, 1 female); Utinga, Pará (USNM, 1 male).

A. i. infuscatus (50 males, 33 females).—BOLIVIA: Cojiba, 12–20 km SW, Pando (LSUMZ, 6 males, 6 females). COLOMBIA: Caño Yerly, Meta (FMNH, 1 male); Guamués, Estación de Bombeo, Putamayo (FMNH, 1 male); San Antonio, Putamayo (FMNH, 2 males, 1 female). ECUADOR: Limoncocha, Napo (LSUMZ, 3 males, 2 females); Sucumbios Province (ANSP, 3 males, 2 females); Taisha, Morona-Santiago (ANSP, 3 males, 2 females); Zancudo Cocha, Napo (ANSP, 1 male, 2 females). PERU: Calientillo, Loreto (FMNH, 2 females); Ccollpa, Río Tambopata, Madre de Dios (FMNH, 1 male); Cordillera de Pantiacolla, E slope at base, Madre de Dios (FMNH, 1 female); Cordillera de Pantiacolla, E slope near summit, Madre de Dios (FMNH, 1 female); Iquitos, S bank 40 mi. E, Loreto (FMNH, 2 males, 1 female); Libertad, 1.5 km S, Loreto (LSUMZ, 4 males, 2 females); Puerto Arturo, Loreto (FMNH, 1 female); Puerto Bermudez, Pasco (FMNH, 1 male); Puerto Maldonado, 105–110 km on road to Quincemil (LSUMZ, 4 males, 2 females); Puerto Yessup, Pasco (ANSP, 5 males); Quebrada Sucusari, Loreto (LSUMZ, 2 males, 3 females); Refugio Juliaca, Madre de Dios (LSUMZ, 3 males); Río Colorado, mouth, Madre de Dios (FMNH, 1 male); Río Manití, Loreto (ANSP, 1 male); Río Shesha, Ucayali (LSUMZ, 3 males, 3 females); Río Yanayacu, Loreto (LSUMZ, 3 males, 2 females).

A. i. purusianus (28 males, 12 females).—BRAZIL: Arimã, Amazonas (CM, 2 males; FMNH, 1 male); Caviana, opposite Manacapuru, Amazonas (CM, 2 males, 2 females; YPM, 1 male, 1 female); Huitanaã, Amazonas (CM, 5 males, 4 females; FMNH, 1 male; YPM, 2 males, 1 female); Nova Olinda, Amazonas (CM, 2 males; YPM, 1 male); São Paulo de Olivença, Amazonas (CM, 7 males, 2 females; YPM, 2 males, 1 female); Tonantins, S bank Solimães, Amazonas (YPM, 2 males, 1 female).

A. i. cervicalis (25 males, 13 females, 1 sex unknown).—BRAZIL: BV-8, 6 mi E on Venezuela border, Roraima (FMNH, 1 male); Mazagão, Amapá (LACM, 1 male); Mucajai River S of Boa Vista, Roraima (LACM, 1 male); Obidos, Pará (CM, 2 males, 2 females); Porto Platon, Amapá (USNM; 1 male, 1 female); Rio Aracauá, Amapá (CM, 2 males, 1 female; YPM, 1 male); Serra do Navio, Amapá (FMNH, 1 female; USNM, 5 males, 2 females); Sorocaima, Roraima (FMNH, 2 males). FRENCH GUIANA: Mana River, Fleuve (CM, 4 males, 3 females); Tamanoir, Saut (CM, 2 males, 1 female; YPM, 1 male, 1 female). GUYANA: Boundary Camp, Acarai Mountains (FMNH, 1 male). SURINAME: Kayser Gebergte Airstrip (FMNH, 1 sex unknown); Neger Kreek (YPM, 1 female); Wilhelmina Mountains, West River (FMNH, 1 male).

A. i. badius (38 males, 18 females, 1 sex unknown).—BRAZIL: Maluracá, Canal at mouth, Amazonas (USNM, 2 males); Membeca, Amazonas (CM, 10 males, 7 females); Panela de Onça, Cachoeira, Amazonas (USNM, 1 male); São Gabriel da Cachoeira, Amazonas (USNM, 2 males, 1 female); Serra Imeri, Amazonas (ANSP, 1 male; USNM, 3 males); Tonantins, Amazonas (CM, 9 males, 3 females). COLOMBIA: San Felipe, Guainía (USNM, 1 male). VENEZUELA: Caño Caripo, Amazonas (USNM, 1 female); Cerro Duida, Amazonas (USNM, 1 female); Cerro de la Neblina, Amazonas (FMNH, 2 males, 1 female); Cerro Marahuaca, Amazonas (USNM, 1 female); Cerro Yapacana, Amazonas (USNM, 1 male, 1 female, 1 sex unknown); Río Caura, Bolívar (CM, 4 males, 1 female); Río Vaciva, below mouth of, Amazonas (USNM, 1 male); Río Yatúa, upper Amazonas (USNM, 1 male); San Carlos de Río Negro, Amazonas (FMNH, 1 female).